

digested and erroneous matter that cumber the pages of modern scientific journals. Here it is that you specially need patience. Before you venture to publish anything, take the utmost pains to satisfy yourselves that it is true, that it is new, and that it is worth putting into print. And be assured that this reticence, while it is a kindness to the literature of science, will most certainly bring with it its own reward to yourselves. It will increase your confidence, and make your ultimate contributions more exact in their facts as well as more accurate and convincing in their argument.

The other danger to which I referred as demanding patience is of an opposite kind. As we advance in our career, and the facts of our investigations accumulate around us, there will come times of depression when we seem lost in a labyrinth of detail out of which no path appears to be discoverable. We have, perhaps, groped our way through this maze, following now one clue, now another, that seemed to promise some outlet to the light. But the darkness has only closed around us the deeper, and we feel inclined to abandon the research as one in which success is, for us at least, unattainable. When this blankness of despair shall come upon you, take courage under it, by remembering that a patient study of any department of nature is never labour thrown away. Every accurate observation you have made, every new fact you have established, is a gain to science. You may not for a time see the meaning of these observations, nor the connection of these facts. But their meaning and connection are sure in the end to be made out. You have gone through the labour necessary for the ascertainment of truth, and if you patiently and watchfully bide your time, the discovery of the truth itself may reward your endurance and your toil.

It is by failures as well as by successes that the true ideal of the man of science is reached. The task allotted to him in life is one of the noblest that can be undertaken. It is his to penetrate into the secrets of nature, to push back the circumference of darkness that surrounds us, to disclose ever more and more of the limitless beauty, harmonious order, and imperious law that extend throughout the universe. And while he thus enlarges our knowledge, he shows us also how nature may be made to minister in an ever augmenting multiplicity of ways to the service of humanity. It is to him and his conquests that the material progress of our race is mainly due. If he were content merely to look back over the realms which he has subdued, he might well indulge in jubilant feelings, for his peaceful victories have done more for the enlightenment and progress of mankind than were ever achieved by the triumphs of war. But his eye is turned rather to the future than to the past. In front of him rises the wall of darkness that shrouds from him the still unknown. What he has painfully accomplished seems to him but little in comparison with the infinite possibilities that lie beyond. And so he presses onward, not self-satisfied and exultant, but rather humbled and reverential, yet full of hope and courage for the work of further conquest that lies before him.

Such is the task in which you may be called to share. When you have entered upon it and have learnt something of its trials and responsibilities, as well as of its joys and rewards, you will look back with gratitude to the training you received within the walls of this College. You will feel even more keenly than you do now how much you owe to the patient kindness and educational skill of your teachers and to the healthy stimulus of contact and competition with your class-fellows. Most heartily do I wish you success in your several careers. Following up the paths which have been opened for you here, may it be yours to enlarge still further the circle of light which science has gained, and to wrest from nature new aids for the service of mankind.

THE BRITISH ASSOCIATION.

BRISTOL MEETING.

SECTION K (BOTANY).

OPENING ADDRESS BY PROF. F. O. BOWER, SC.D., F.R.S.,
PRESIDENT OF THE SECTION.¹

III.

THE following considerations influence me in forming an opinion as to the real place of apospory and apogamy in the history of the alternating generations:—

I. The Bryophytes show remarkable uniformity of alternation:

¹ Continued from p. 91.

irregularities are few; apogamy is not recorded; apospory appears rarely, as a physiological refuge for the destitute plant. This uniformity goes along with the protected and dependent condition of the sporophyte. All Pteridophytes have their embryos protected while young, and this seems to have been their primitive condition. The true lesson of the Bryophyta, which include the simplest living Archegoniates, seems thus to be that uniformity of alternation goes with a simple structure, and a protected or dependent condition of the sporophyte; and this we have reason to believe was the condition of the simpler Archegoniate fruits.

II. The distribution of apogamy and apospory among Archegoniates at large is very irregular; the Leptosporangiate Ferns are the headquarters; but they are a peculiarly specialised phylum, with free sporophyte, exposed when mature, though protected while young. They are adapted to special conditions and show a greater plasticity of development than any other Pteridophytes. The Ferns are subject to other abnormalities than apospory and apogamy. The root may develop directly into a shoot, or the apex of the leaf into a bud. I think it has been too readily held that the Ferns occupy a special place as a key to the morphological problem. We should bear in mind how really isolated they are; they are essentially an extreme, even an extravagant type; they show the largest sporophylls in the whole vegetable kingdom, with the largest numerical output of spores from each. Many are specialised in accordance with extreme conditions of shade and moisture. These considerations should temper our view of them, not only as material for normal comparison, but also as exponents of abnormality.

III. The fact that in cases of induced apogamy in Ferns archegonia are first produced, clearly shows that in these cases the first intention of the plant is towards a normal production of embryos, while apogamy takes its place as a substitutionary growth. It may remain an open question how far direct apogamy will bear a similar interpretation.

IV. The character of the aposporous and apogamous growths is very anomalous; their position is not definite; aposporous growths may arise from the sorus and sporangia, or from the most varied points on the margin or surface of the leaf. With regard to apogamy in Ferns, it appears, as the result of a large number of observations, that though there is an average normal of position, still any one part of the sporophyte—stem, leaf, ramentum, root, sporangium, or even tracheid—may arise, independently of others, from the prothallus. Single sporangia, or groups of them, may appear without vegetative organs of the sporophyte; leaves without other parts; in one case, I believe, as many as ten roots have been seen without any other members of the sporophyte! The close similarity of the parts thus irregularly placed to those formed in regular sequence in the normal plant should be a warning of their abnormality. I cannot see in them any suggestion of a primitive state. Dr. Lang tells me that these exceptional developments form only a small proportion of the individuals in any one culture; still they are there, and those who hold that apogamous developments are a suitable basis for morphological argument must not pick and choose those cases which suit their views, but must take even the most extravagant into careful estimation. My own view is that these anomalous growths are not a safe guide to past history. But looked upon as the result of a recently acquired transition from one generation already established to the other, following nuclear changes, in the one case of reduction after insufficient nutrition, in the other of doubling of the chromosomes following on plethora, apospory and apogamy are at least intelligible. We shall understand how the transition may take place at one point or at many, while the irregularity of the parts produced offers no morphological difficulty; it is rather what might have been anticipated if the transition were a ready consequence of the conditions we have noted.

Lastly, a word on Dr. Scott's utilitarian argument. He remarks, "a mode of growth which affords a perfectly efficient means of abundant propagation cannot, I think, be dismissed as merely teratological." We must be clear that utility is no certain evidence of antiquity. As refuges for the physiologically destitute, apogamy and apospory may play an important part now, and in so far are not to be dismissed as mere freaks of nature. But in my view they would rank, as regards utility pure and simple, with the formation of adventitious buds on the root-system of a Poplar that has been felled; or with the bulbils which replace the flowers in so many mountain species; neither

these, nor, I think, aposporous or apogamous growths, throw any direct light upon the story of descent.

To sum up then, not only do I find that the facts in our possession, including the wildest anomalies, are consistent with an antithetic theory, but a comparison of normal forms seems to me to support the opinion that the sporophyte has appeared as the result of gradual elaboration from the zygote, a fresh phase having been thus gradually intercalated in the course of evolution. This idea first clearly stated by Celakovsky in 1868, was developed by him in subsequent writings. I endeavoured to place it on a footing of adaptation to external conditions, in 1890; and in 1897 we find Strasburger restating the position in terms almost identical with my own, but upon a basis of nuclear detail which had not been dreamed of when the view was first propounded. Dr. Scott has enthusiastically appreciated the double verification of the forecasts of Prof. Pringsheim; I think that the way in which the antithetic theory is found to work in with the nuclear details recently discovered appeals quite as strongly to my mind.

In the course of this discussion I have not been anxious to point out such difficulties as beset the homologous view; all I have attempted here has been to set aside some of the difficulties which have been suggested in opposition to an antithetic view, and to show that the latter theory will adequately cover the facts.

Returning now to our general inquiry on homology, we see that on the antithetic view the two generations are not *homogenetic*; but they may be in a high degree *homoplastic*, and this homoplasmy may be impressed upon the two generations, even in the same species, as in some Lycopods. I have never felt the cogency of the fact that the gametophyte of *L. cernuum* is somewhat similar in outline to the young sporophyte. Both generations are exposed to similar circumstances, and may be reasonably expected to have reacted alike. Moreover, the similarity of form of the "leaves" of prothallus and planus is but slight, and is not maintained in allied species. Their arrangement is variable. Between them also lies the essential structural difference, so widespread among Archegoniate plants, that in the sporophyte stomata and intercellular spaces are present, in the gametophyte they are absent. These are just such differences as point to homoplastic development. More commonly, however, the homoplastic development is only seen in distinct organisms, and in this sense we shall rank the leaf of the Moss as the homoplast, but not the homogene, of the leaf of a Lycopod or of a Fern.

THEORY OF THE STROBILUS.

Some years ago I submitted to the Section a theory of the strobilus in Archegoniate plants. Comparisons were drawn between Pteridophytes and Bryophytes, and it was suggested that the origin of the strobilus of the former was "from a body of the nature of a sporogonial head." I specially pointed out at the time that my object was not a mere hunt after homologies, but to obtain some reasonable view of the methods of advance in Archegoniate plants. I wish to lay special stress upon this, for some appear to think that by denying an homology which I have not been at pains to maintain, they invalidate this search after the methods of advance. The Bryophytes as we now see them are our best guides in the search after these methods, even though they may not have been in the direct line of descent of Vascular Plants. As regards the comparison of the strobilus with a sporogonial head, I wish to make it clear that a Moss sporogonium is not specially indicated. The expression used has been "the origin of the strobilus from a body of the nature of a sporogonial head"—that is simply a part of the sporophyte which bears spores internally as distinct from a lower vegetative region. We see in more than one sequence of Bryophytes how in a sporogonial head, as thus defined, the spore-production becomes restricted in extent, and relegated towards a superficial position by the formation of a central sterile mass. I am ready to join Dr. Scott in his confession of inability to find anything like an intermediate form between the spore-bearing plant of the Pteridophyta and the spore-bearing fruit of the Bryophyta, and to agree that at the best there is nothing more than a remote parallelism not suggestive of affinity; but none the less I think we should continue to search among the Bryophyta for suggestions as to the methods of advance, and to have confidence in transferring these ideas across the gulf, for I believe this to be both a reasonable and a promising method of study.

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DORSIVENTRALITY.

Interesting questions arise in connection with dorsiventral structure. In the Equisetineae, and almost all Lycopodineae, the strobilus is of the radiate type, therein corresponding to the radial structure of typical sporogonia. While certain Ferns are of the radiate type, others are conspicuously dorsiventral, even from their earliest embryonic state. Dorsiventral structure also appears in the vegetative region, and sometimes, though rarely, in the strobilus of *Selaginella*. Prof. Goebel, in a chapter of his "Organographie," the publication of which may be recognised as the leading event in the morphological studies of the year, discusses the origin of the dorsiventral state in a number of examples, and his results have a most interesting bearing on our theory of the strobilus.

He shows in the case of *Vaccinium Myrtillus* how the first shoot of the seedling is orthotropic and radial; the lateral shoots, formed after the apical growth of this is arrested, are also orthotropic, but the lateral shoots of higher order become plagiotropic with leaves in two lateral rows. He points out the intermediate steps from one condition to the other, and how finally the growing point itself is influenced by the external agency (apparently light), which leads to a change of the leaf-arrangement. This seems to be the case in many other Phanerogamic plants.

A particularly interesting account is also given of similar changes in *Selaginella*. Some eight species are orthotropic, radial, and isophyllous. *S. sanguinolenta* shows a direct response to external conditions, being upright and isophyllous in bright and dry situations, plagiotropic and anisophyllous in damp and shady situations. The bulk of the genus are, however, either plagiotropic and anisophyllous throughout, or some may have an early orthotropic stage. But he concludes that even in "habitually" anisophyllous *Selaginellas* we have to do with an adaptive character, induced probably by light.

We see then good evidence that in certain cases the dorsiventral shoot is a result of adaptation, and the radial probably the primitive. Was this always so? We need not discuss the case of the gametophyte, as the problem there is even more varied and difficult, and does not at the moment engage our attention. But the question whether in the sporophyte the radial was in all cases the primitive type is clearly related to our theory of the strobilus. The sporogonia of Bryophytes are, with few exceptions, orthotropic, and almost uniformly radial; exceptions such as *Diphyscium* and *Buxbaumia* have been shown to have an interesting relation to the incidence of light, and are readily recognised as derivative. The distinctively strobiloid Pteridophytes mostly maintain this radial structure; this may be so both in strobilus and vegetative organs, as in *Equisetum*, *Isoetes*, in most species of *Lycopodium*, and in some *Selaginellas*; or the vegetative region may be dorsiventral, and the strobilus return to the radial type, as in some species of *Lycopodium* and most *Selaginellas*; but in some *Selaginellas* even the strobilus may be dorsiventral.

In the Ferns the case is less obvious; the large size of the leaves, combined often with a dorsiventral structure of the shoot, makes a comparison with a radial strobilus less easy. Goebel has pointed out that in many dorsiventral Ferns the dorsiventrality is already defined in the *punctum vegetationis*, and does not depend upon a subsequent shifting of the parts. But it should be remembered how many Ferns are orthotropic and radial; that almost all the large genera include species with simple unbranched leaves. Further, the series of the Ophioglossaceae, possibly a distinct phylum from the true Ferns, may be held to illustrate a progressive elaboration of the leaf, from smaller leaved forms which are orthotropic and radial, to larger-leaved forms, which are sometimes orthotropic and radial (*Botrychium*), sometimes plagiotropic, and dorsiventral (*Helminthostachys*). It is not, I think, improbable that these, and also the true Ferns, are referable in origin to an orthotropic strobiloid type, with radial structure. This opinion was in substance suggested in 1894 at Oxford; these recent observations of Goebel on the derivative nature of dorsiventral shoots strengthen the position then taken up, while they supply us with fresh examples of homoplastic development.

CONCLUSION.

This discussion was entered on with a view to finding whither phylogeny as a basis of morphology would lead us. However unprepared we may be to pursue it with certainty into detail, or

to apply a terminology to the sequences which we recognise, we must, I think, accept phylogeny as the natural basis for morphology. I do not think that any middle course between this and an artificial system is possible or reasonable. But here we launch ourselves upon a sea of uncertainties on which we must keep our course with care. Following it, we think we espy certain great movements in nature. We may recognise what we believe to be a true evolutionary sequence, but who is to say whether it is a progressive or a retrograde sequence? It may be even one divergent from some middle point. Our best friend may read the sequence in opposite order to ourselves and arrive at a diametrically opposite conclusion. There is no finality to this judging of probabilities, a fact which should be always before the mind, especially in the warmer moments of discussion.

It is interesting to trace the parallel between the progress of classification of plants as a whole, and that of the classification of their parts. In each case the earlier systems were artificial. We may compare the Linnaean system of taxonomy with the Hofmeisterian organography: in both the rigid application of a preconceived method placed incongruous things in juxtaposition, in each case a widening of the basis of the classification has resulted in a redistribution on more natural lines. The present ideal of taxonomy is the same as that of the phylogenetic organography, viz. to group according to descent. The limitations are alike: systematists and morphologists both find their greatest difficulty in the incompleteness of the record, and the frequent isolation of the thing to be classified.

But without following the obvious parallel further, we may now briefly review our position as regards organography, and the following categories are to be recognised, though they graduate almost imperceptibly into one another:—

Homogeny.—(a) *Repetition* of the individual part in successive generations, with the same number and position. This is exemplified by the cotyledons, the foot, and first root.

(b) *Essential correspondence* of parts varying in number and position, but corresponding in character and development, produced in a regular sequence; e.g. most cases of continued embryology.

(c) *Transferred position* of parts, similar in origin and structure to those produced in regular sequence; e.g. roots, adventitious buds, sori of *Aspidium anomalum*, aposporous and apogamous growths, many monstrosities; these we may believe to result from a transfer of inherited developmental capability.

Homoplasmy.—This may be recognised with varying degrees of probability; starting from cases where the question of community of descent is open (as with nearer circles of affinity), and proceeding to those in which distinct evolution is virtually certain. It remains for future investigation to clear up doubtful points. Meanwhile, taking the case of leaves for the purpose of illustration, we may contemplate the following possibilities:—

(a) A possible origin of two homoplastic series of leaves in the same plant, and the same generation (*Phylloglossum*).

(b) Two homoplastic series in the same plant, but in different generations (*Lycopodium cernuum*).

(c) A possible distinct origin of homoplastic leaves in distinct phyla, but in the same generation (sporophyte of Ferns, Lycopods, Equiseta).

(d) A distinct origin of homoplastic leaves in distinct phyla, and distinct generations (e.g. leaves of Bryophyta and of Pteridophyta).

Now *Homology* has been used in an extended sense as including many, or even all, of these categories. It seems plain to me that this collective use of the term homology carries no distinct evolutionary idea with it; it indicates little more than a vague similarity; the word will have to be either more strictly defined or dropped. The old categories of parts based upon the place and mode of their origin are apt to be split up if the system be checked by views as to descent. Comparison, aided by experiment, supersedes all other methods, and the results which follow raise the question of terminology of parts which have arisen by parallel development.

In parts which are of secondary importance, such as stipules, pinnae, the indusium, hairs, glands, the inconstancy of their occurrence points to independent origin by parallel development in a high degree; in parts of greater importance, such as leaves, a parallel development may also be recognised, though in a less high degree; in the case of sporangia their acceptance

as a category *sui generis* dispelled the old view of their various origin from vegetative parts; but we must remember that this does not by any means exclude a parallel development also in them, by enlargement and septation from some simpler spore-producing body, though this is not yet a matter of demonstration. Finally, the sexual organs are probably homogenetic in all Archegoniate plants, but we have no proof that sexuality arose once for all in the lower plants; the probability is rather the contrary. Thus we may contemplate as very general a polyphyletic origin of similar parts by evolution along distinct lines, but resulting, it may be, in forms essentially similar.

There are two extreme courses open to those who wish to convey clearly to others such matters as these; the one is to use a separate term for each category of parts, which can be followed as maintaining its individual or essential identity throughout a recognised line of descent—in fact, to make a polynomic terminology of members run parallel with a polyphyletic development. The other course is to make it clear always in the use of terms applied to parts, that they do not convey any evolutionary meaning, and to use them only in a descriptive sense. Perhaps the former is the ideal method, and it may be a desirable thing, as polyphyletic origins of parts become more established, that the terminology should be brought to reflect at least the more important conclusions arrived at. How this may be done we leave for the future to decide, though I have indicated a first step in the case of the leaves of Mosses and Ferns.

But, for the present, the whole matter is still so tentative that it is well to be content with something which falls short of the ideal, and to maintain the usual terms, such as stem, leaf, root, hair, sporangium, &c., as simply descriptive of parts which correspond as regards general features of origin, position, and nature; but with no reference either, on the one hand, to conformity to any ideal plan, or, on the other, to any community by descent—in fact we shall preserve the original pre-Darwinian sense of these words, which was purely descriptive, and avoid any attempt to read into them any accessory meaning.

A special interest attends those cases of transfer of inherited developmental capability where a part appears with its normal characters, but in a position which is not usual, such as the transfer of the sori of *Aspidium anomalum*; comparable with these transfers on the one hand are those apogamous growths where roots, leaves, ramenta, sporangia may arise independently out of the usual succession. These may be compared, on the other hand, with those interpolations of extra parts, such as the accessory stipules in the stellate Rubiaceae, the extra stamens in Rosaceae, &c. We are unable as yet to say what it is which determines the position and mode of origin of parts; I do not myself think that Sachs's hypothesis of "Stoff and Form," involving ideas of material differences which have not been demonstrated, will advance the question so much as a careful following of the details in the origin of the parts, say in some of these apogamous growths. Here we see the plant body in a sense analysed before us; any one part may be produced separately from any other. An elucidation of how any one of these is initiated and determined should lead to a knowledge of the influences which act also in the normal sequence, and determine the origin of parts in the plant body at large.

I have attempted to touch upon some of those questions in the Morphology of Plants which specially interest us at present, and I dare say in doing so have revealed to you some of the special weaknesses of this branch of the science. The want of finality in this unravelling of history without documents, the ample latitude for difference of opinion, according to the relative weight attached by one or another to the same facts: these are difficulties inherent in the very nature of our study, while to many minds they increase rather than diminish its attractions. Nevertheless the progress of morphology in late decades has plainly been towards a truer appreciation of how divers forms have originated, and so towards a better recognition of affinities. Seeing that this is clearly the main trend, we may take heart as to the advancement of morphological knowledge. We shall not allow ourselves to be deterred by reason of the want of finality or the deficiency of evidence, however strongly we may feel the weight of these difficulties. We shall rather try to make the best of such evidence as we possess, with the full confidence that, however insoluble the problem of descent may really be, inquiry along scientific lines will at least lead us nearer to the goal.